

Contrasting patterns of seed dispersal between alien mammals and native lizards in a declining plant species

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Abstract

The introduction of carnivorous mammals has led many native island species to extinction. In the Balearic Islands, the introduction of carnivorous mammals in the main islands have contributed to the extinction of the endemic lizard *Podarcis lilfordi*, which is an important seed disperser of many plant species. One of the introduced mammals, *Martes martes* (pine marten), is also known to disperse seeds and may replace the native lizard in this role in islands. However, little is known on the patterns of seed dispersal by these two different species and their possible implications for plant regeneration ability and population structure. We have compared the quality of seed deposition provided by both to the vulnerable Mediterranean shrub *Cneorum tricoccon*, by studying the pattern of seed distribution among sites generated by both dispersers as well as the suitability of those sites for seedling emergence and establishment. The study was carried out in two types of habitats (coastal shrublands and pine forests) and two islands (Mallorca and Dragonera). Lizards and mammals showed contrasting patterns of seed deposition and, where lizards were absent, mammals played their role as seed dispersers in pine forests but not in coastal shrublands. The lack of seed dispersal in the coastal shrubland seriously limits recruitment, by concentrating seeds under conspecifics and hindering colonization opportunities, marking a long-term trend towards decline. The introduced predator replaces the native seed disperser in its service where it has gone extinct, although with important differences in the dispersal service provided.

Key-words Balearic Islands, *Cneorum tricoccon*, mutualism, saurochory, seed dispersal disruption, seedling recruitment.

Introduction

Seed dispersal is a key process in the reproductive cycle of a plant. The seed dispersal effectiveness provided by an animal refers to its contribution to plant recruitment and is a key concept in the study of plant-animal interactions. It has a quantitative and a qualitative component: (1) the quantity of dispersal refers to the number of seeds dispersed and (2) the quality of dispersal refers to the probability of recruitment of each dispersed seed (Schupp 1993; Schupp et al. 2010). The estimation of seed dispersal effectiveness can be arduous, especially regarding the qualitative component, and for this reason, there are few studies that provide comprehensive assessments (e.g. Rey and Alcántara 2000; Traveset et al. 2003; Calviño-Cancela and Martín-Herrero 2009). A crucial aspect of the quality of a seed disperser is the pattern of seed distribution among microhabitats. Animals may differ substantially in their patterns of habitat use which may result in contrasting seed dispersal patterns (Calviño-Cancela 2002; Martínez et al. 2008). In addition, different microhabitats provide seeds with contrasting suitabilities for recruitment. The suitability of microhabitats of seed arrival has the potential to neutralize or enhance the effect of a disperser on the quantitative component, specifically when an animal deposits a high proportion of seeds in sites where the probability of recruitment is low (Schupp 1993; Schupp and Fuentes 1995; Schupp 2007; Calviño-Cancela and Martín-Herrero 2009). Classically, microhabitat suitability is estimated as the product of the transition probabilities between the different stages of the regeneration process, from seed dispersal to seedling establishment. Seeds and seedlings are highly vulnerable to mortality, which makes it especially important to assess microhabitat suitability during these critical early stages (Harper 1977; Herrera et al. 1994; Calviño-Cancela 2007). Assessing microhabitat suitability for seedling emergence can be significantly less costly using seedling-to-seed

ratios (i.e. the number of seedlings recruited divided by the number of seeds arrived) to estimate the probability of seedling recruitment at different sites. This method saves time and simplifies the study of the demographic consequences of seed dispersal and the effectiveness of dispersers (see Calviño-Cancela 2011a).

Seed dispersal systems are usually generalized and mutual dependences between interacting plants and animals are usually weak (e.g. Bascompte and Jordano 2007). On islands, however, communities are often depauperate, and plants have been shown to be more specialized in their dispersers than in the mainland (Olesen and Jordano 2002; González-Castro et al. 2012). Thus, plants dispersed by only one or a few animals seem to be more common in island systems. This increases plant vulnerability to eventual declines or extinctions of the animal partner, which may lead to mutualism disruptions (Riera et al. 2002; McKinney et al. 2009, Rodríguez-Pérez and Traveset 2012; Traveset et al. 2012). A major cause of mutualism disruptions on islands is the introduction of alien species (Traveset and Richardson 2006). For instance, the introduction of non-native predators may lead to the extinction or severe decline of island species, some of which have important roles as seed dispersers (Mortensen et al. 2008; Kelly et al. 2010). The invaded ecosystem thus loses the ecological function played by the extinct species. On the other hand, the newcomers may establish new interactions with the local community and play some of those lost functions. Predators and preys hardly play similar ecological roles, but predators such as carnivorous mammals are often effective seed dispersers (Herrera 1989; Rosalino and Santos-Reis 2009) and may replace in this role those species they have contributed to wipe out.

In the Balearic Islands, the endemic lizard *Podarcis lilfordi* (Lacertidae; Günter 1874) plays an important role as pollinator and seed disperser of many plant species (Traveset and Sáez 1997; Traveset and Riera 2005). The introduction of carnivorous

mammals in the main islands seems to have led this lizard to extinction (Reumer 1984; Pérez-Mellado et al. 2008), and nowadays it is only present in small islands and islets where introduced carnivores are absent (Terrasa et al. 2009). Paradoxically, some of these introduced mammals replace the endemic lizards as seed dispersers of some plant species. This is the case of *Cneorum tricoccon* L., which is mainly dispersed by the native lizard *P. lilfordi*, (Traveset 1995a), and by the introduced pine marten *Martes martes* L. (Riera et al. 2002; Traveset et al. 2012). Previous studies suggest that lizards remove more fruits and that recruitment is higher in populations with lizards, but little is known about the quality of these two animals as seed dispersers.

The aim of this study is to assess the quality of seed dispersal provided by *P. lilfordi* and by *M. martes* to *C. tricoccon*, examining the pattern of seed distribution among sites generated by both dispersers as well as the suitability of those sites for seedling emergence and establishment.

Materials and methods

Study species

Cneorum tricoccon L. (Rutaceae) is a perennial shrub ~ 1 m in height (up to 2 m). It is distributed along the Western Mediterranean Basin and is mainly present in Mediterranean coastal shrublands on calcareous soils and in Mediterranean woodlands dominated by oaks and pines (suppl. mat. in Traveset et al. 2012). In the Balearic Islands, it is present on nine islets (<1000 ha) and in the small island of Cabrera. In the larger islands of Mallorca and Menorca it seems to have declined and is restricted to a few sites. Thus, fossil seeds of *C. tricoccon* found in Menorca in Pliocene deposits, in localities where the species is no

longer present, demonstrate a more widespread distribution in the past (Traveset et al. 2005) and a drastic population decline in Menorca has been observed in the last years (Traveset, unpub. data). It has been categorized as vulnerable (IUCN, 2001).

It is an andromonoecious insect-pollinated plant with a long flowering period, from October to early June. Fruits are composed by three red cocci (locules of a syncarpous ovary), each being a drupe. Ripen fruits are available from mid-March to June, and unconsumed fruits remain undispersed on the plants for long periods (~1 year) (Traveset 1995b). Fruit consumption by passerine birds has not been observed, despite the suitable size and attractive colour of fruits for birds, which could be related to the high amount of secondary compounds (Traveset, unpubl. data). However, a few seeds of *C. tricoccon* have been found in gulls' regurgitations, which suggest that they disperse this species (Calviño-Cancela 2011b).

Study sites

The study was carried out at the Balearic Islands (western Mediterranean Sea), in Mallorca island (39°58'N, 3°08'E, 364 011 ha) and on Sa Dragonera islet (39° 35' N, 2° 19'E, 2 880 ha), located 2 km off the NW coast of Mallorca. Mean annual rainfall is 430 mm in Mallorca and 350 mm in Sa Dragonera. Average annual temperatures are similar in Mallorca and Sa Dragonera (17-18°C). July and August are the hottest months, with average maximum temperatures of 29-30°C, while January and February are the coldest, with average minimum temperatures of 8-8.5°C (Spanish Agency of Meteorology, www.aemet.es). In Mallorca, *P. lilfordi* has become extinct, which occurred, according to the fossil record, after the introduction of a number of carnivorous mammals (mostly pine martens, weasels, genets and cats) presumably during the Roman expansion, c. 2000-2500 years ago (Pérez-Mellado 2002, Alcover

2008 and references therein). In Dragonera, there are no carnivores and *P. lilfordi* is still present and abundant (Pérez-Mellado 2002).

In each island we chose two populations, one in each type of habitat: the coastal shrubland and the pine forest. The vegetation in the coastal shrubland was dominated by the shrubs *Pistacia lentiscus*, *Olea europaea*, *Ephedra fragilis*, *Phyllirea spp.* and *Cistus spp.* In pine forests, *Pinus halepensis* was the dominant tree and the understory was composed by an assemblage of shrubs similar to the coastal shrubland. The percentage of area covered by *C. tricocon* was similar in the four study sites ($3.8 \pm 1.6\%$ and $4.2 \pm 1.7\%$ in the coastal shrubland and the pine forest in Dragonera, and $5.5 \pm 2.1\%$ and $3.4 \pm 0.93\%$ in the coastal shrubland and the pine forest in Mallorca, respectively; as measured in 10 transects, 10 m long x 0.5 m wide).

Spatial distribution of animal faeces and seedlings

In May 2010, we recorded the distribution of seed disperser faeces (Lizards and mammals) and seedlings among habitats and microhabitats in 10 transects (10 m long x 0.5 m wide) in each of the four study sites. Microhabitats were grouped in the following categories at coastal shrubland sites: 1) open ground, 2) under *C. tricocon*, 3) under *C. tricocon* associated with other shrubs, 4) herbs and grasses 5) rocks. At pine forest sites, the same categories plus an additional one, 6) open under canopy, were considered. Lizards of the species *P. lilfordi* are the only seed dispersers at Dragonera Islet and *M. martes* is the only mammal species in Mallorca, in this case due to the low density of faeces, an additional search with 30 transects (same dimensions) was carried out in the pine forest in Mallorca (the only population where this carnivore is present in the study) in February and April 2012.

Site suitability

For the three main microhabitats at each habitat (those receiving more seeds and/or concentrating more seedlings), we estimated their suitability for seedling emergence and seedling survival by computing the seedling/seed ratio and the ratio between established seedlings and recently emerged seedlings, respectively. In coastal shrublands, the main microhabitats were: 1) open ground, 2) under *C. tricocon* and 3) under *C. tricocon* associated with other shrubs (to assess whether there was a nursery effect from other shrubs on *C. tricocon* seedlings), whereas in pine forests, the chosen microhabitats were: 1) open ground, 2) open ground under canopy and 3) under *C. tricocon*. We established 10 permanent plots (50 x 50 cm) in each site to measure seed and seedling density. Seed density was assessed by collecting soil samples with a corer 9 cm in diameter and 5 cm in depth. We sieved these samples, recording all intact seeds and those damaged by predators. For intact seeds (with no external damage) we assessed seed viability by cutting seeds open and visually inspecting the endosperm and embryo (cutting test, Gunn 2001). At the end of spring (June 2010), before the high seedling mortality usually occurring during the summer drought, we registered the number of seedlings in three size categories (0-5 cm, 5-10 cm and 10-20 cm in height) as well as the number of saplings (> 20 cm). Due to the small number of >10 cm seedlings and saplings, only seedlings in the two smaller categories were used to compute the ratio between seedling stages. The seedling/seed ratio was computed with 0-5 cm seedlings.

Data analysis

The spatial distribution of faeces and seedlings was assessed with Chi-Square tests using Statistica 7.0 (StatSoft 2004) in order to determine whether they were randomly distributed among microhabitats (distributed according to the percentage cover of microhabitats) or otherwise appeared preferentially at certain microhabitats.

The samples of seed and seedling densities were bootstrapped and seedling/seed ratios and ratios between seedling stages were then computed by dividing randomly selected bootstrapped replicates of seedling density by seed density samples, and those of established seedlings (5-10 cm) by newly emerged seedlings (0-5 cm), respectively. Invalid values (when a nonzero number of seedlings or of older seedlings, respectively, was divided by null seeds or null recently emerged seedlings, respectively) were replaced by new calculated values, until we obtained 500 valid values (values higher than or equal to 0; see Method III in Calviño-Cancela 2011a).

In order to determine whether there were differences between sites in seed or seedling density and in site suitability, we used nested Generalized Linear Models (GLM) to evaluate the effect of island, habitat and microhabitat type (with habitat nested within island and microhabitat nested within habitat) on seed density (total, viable and predated), seedling density, seedling/seed ratio and the ratio between seedling stages. We used the quasi-poisson distribution, as this distribution provided the best fit to our data. For these analyses, we used R (R-project 2.8, R Development Core Team 2008).

Results

Distribution of animal faeces

In Dragonera, the density of *P. lilfordi* faeces did not differ significantly between habitats (coastal shrubland vs. pine forest; $t_{18} = 0.64$; $P = 0.531$), and had a non-random distribution among microhabitats in both cases (coastal shrubland: $\chi^2_4 = 105.9$; $P \leq 0.001$ and pine forest: $\chi^2_5 = 121$; $P \leq 0.001$; Fig. 1). Rocks and open ground outside the pine canopy were the most used microhabitats by *P. lilfordi*, both in the coastal

shrubland and the pine forest (Fig. 1). By contrast, open ground under the pine canopy, herbs and shrubs, including *C. tricocon*, received fewer faeces than expected, with no faeces being found under *C. tricocon* in the pine forest. In Mallorca, no faeces of *C. tricocon* seed dispersers were found in the coastal shrubland. In the pine forest, however, we did find *M. martes* faeces, which were not randomly distributed across microhabitats ($\chi^2_5 = 44.80$; $P \leq 0.001$). These faeces were most abundant in the open, both below and outside the pine canopy, and rocks were also a relatively frequent microhabitat for *M. martes* defecation (Fig. 1).

Total, predated and viable seeds in the seed bank

Total seed density was significantly higher in Dragonera than in Mallorca, and the percentage of seed predation was significantly higher in Dragonera (50 %), resulting in a similar density of viable seeds in both islands (Table 1, Fig. 2). In Dragonera, the coastal shrubland had a significantly higher density of viable and total seeds than the pine forest (Table 1, Fig. 2), whereas in Mallorca there were similar seed densities (viable, predated and total seeds) between habitats. Differences in seed density among microhabitats were not significant in any island and habitat, despite the absence of seeds in open ground in the coastal shrubland in Mallorca (Table 1, Fig. 2).

Distribution and density of seedlings

As for seeds, seedling distribution was not random among microhabitats, i.e. it was different than expected according to their cover ($\chi^2_4 \geq 59.6$; $P \leq 0.001$; Fig. 1). In both islands and habitats there were more seedlings than expected under *C. tricocon*, especially in the coastal shrubland in Mallorca. In this island, no seedlings were found in open ground in the coastal shrubland, and there were less seedlings than expected in the pine forest outside the pine canopy, but more than expected under the canopy. In

Dragonera, by contrast, there were more seedlings than expected in open ground in both the coastal shrubland and the pine forest (both under and outside the pine canopy; Fig. 1). All other microhabitats had few seedlings (less than expected).

Regarding differences in seedling density among sites, they were not significant between islands but differed between habitats in both islands, being significantly higher in the coastal shrubland than in the pine forest (Table 2, Fig. 2). Moreover, there were no differences in seedling density among microhabitats in the pine forest (Fig. 2). By contrast, significant differences existed among microhabitats in the coastal shrubland in both islands (Table 2, Fig. 2). In Dragonera, both open ground and under *C. tricocon* had the highest seedling density (Fig. 2), whereas in Mallorca there were no seedlings in open ground and most were under *C. tricocon*.

Transition probabilities between life stages

The transition probability between the stages of seed and seedling, as measured by the seedling/seed ratio, was similar between islands but differed between habitats and microhabitats (Table 2). It was significantly higher in the coastal shrubland than in the pine forest in Dragonera, but the pattern was the opposite in Mallorca (Fig. 3). In the coastal shrubland of both islands, this ratio was significantly higher under *C. tricocon* than under *C. tricocon* associated with other shrubs, and in Dragonera it was similar in open ground and under *C. tricocon*. In the coastal shrubland in Mallorca, this ratio could not be estimated in open ground because there were no seeds in this microhabitat. In pine forests, the pattern among microhabitats was similar in both islands, with the highest seedling/seed ratio in open ground under the pines, followed by under *C. tricocon*, and open ground outside the pine canopy having the lowest ratio (Fig. 3).

The transition probability between seedling stages was similar between islands and habitats but differed between microhabitats (Table 2, Fig. 3). In the coastal shrubland of Dragonera, this transition was similarly high in open ground and under *C. tricocon* (Fig. 3). In the coastal shrubland of Mallorca, the highest transition probability was found under *C. tricocon* associated with other shrubs but, again, it could not be assessed in open ground because of the absence of seedlings. In the pine forest, the pattern among microhabitats was similar between islands, with significantly higher suitability under *C. tricocon* and lower in open ground, both under and outside the pine canopy, although the suitability of open ground under the pine canopy was statistically higher than outside the canopy in Dragonera.

Discussion

Seed distribution in endozoochorous species responds to the presence or absence of seed dispersers as well as to their particular movement patterns and habits. In the Balearic Islands, *C. tricocon* depends mainly on *P. lilfordi* as the native seed disperser, but it is also dispersed by introduced carnivorous mammals (Traveset 1995a; Riera et al. 2002). In Dragonera, where the native seed dispersal interaction still persists and *P. lilfordi* reaches a very high density ($729.42 \pm 124.15 \text{ ha}^{-1}$, Pérez-Mellado et al. 2008), it plays a very active role as disperser, as reflected by a high density of faeces with *C. tricocon* seeds both in the coastal shrubland and in the pine forest (see also Riera et al. 2002). In Mallorca, where *P. lilfordi* has become extinct, no animal seed dispersal was detected in the coastal shrubland, but *M. martes* played this role in the pine forest. In Dragonera, in addition to the presence of *P. lilfordi*, it was also noteworthy the high levels of seed predation found (c. 8 times higher than in Mallorca). This is probably

associated with the very high abundance of rats (*Rattus rattus*) in this islet, which are important seed predators (Traveset et al. 2009). However, this did not lead to a lower availability of viable seeds in Dragonera, due to a higher total seed density in this island. Seed density was also higher in coastal shrubland than in the pine forest in Dragonera. These differences in seed density are not related with differences in the density of adult individuals, which is similar in the four study sites. They could be due to differences in fruit production, related to causes not dealt with in this study (e.g. differences between populations in abiotic conditions such as soil nutrients or light availability, or the effectiveness of pollination), or to a more active seed dispersal in Dragonera and in the coastal shrubland in this island, where lizards are present and abundant, as indicated by the higher density of faeces (Fig. 1). A more active seed dispersal results in less fruits being stored undispersed in the canopy compared to populations with lower abundance or absence of dispersers (Riera et al. 2002) and more seeds being in the soil seed bank.

Podarcis lilfordi and *M. martes* have very different physiologies and behaviours, which results in contrasting patterns of seed dispersal. In Dragonera, *P. lilfordi* acts as a seed disperser both in the pine forest and in the coastal shrubland, and deposited seeds mostly in open microhabitats, especially in rocks. This is probably associated with the need of thermoregulation in this ectothermic animal (Bauwens et al. 1996). In relation to this, the low seed dispersal by *P. lilfordi* under the pine canopy in the forest is remarkable, suggesting the need of heat and the avoidance of shade in this cool habitat. *Martes martes*, however, showed a clear preference for this microhabitat, concentrating there the highest density of faeces, which determined a clear contrast in seed distributions between Dragonera (with *P. lilfordi*) and Mallorca (with *M. martes*). *Martes martes* deposited also a relatively high number of faeces in open ground and

rocks, although the density in this former microhabitat was lower than in the case of *P. lilfordi*. Rocks have a high thermal inertia, remaining warm for some time after air temperature drops, which increases their attractiveness for ectothermic lizards. Despite high seed loads on rocks, they are not suitable for seedling recruitment, which is restricted to the small crevices where soil and seeds are trapped. However, seeds deposited on rocks may fall to their surroundings, usually open ground, where they may germinate and enjoy relatively high nutrient concentration due to the accumulation of faeces and dust washed down the rock surface (Jobidon 1993; Traveset et al. 2001).

The extinction of frugivorous lizards has been shown to have important consequences for recruitment of *C. tricocon*, with lower recruitment on islands where lizards have become extinct and have been replaced by carnivorous mammals as seed dispersers (Traveset et al. 2012). Our results complement those obtained by Traveset (1995a) and Riera et al. (2002), related to the quantitative component of effectiveness, which showed higher seed removal in populations where *P. lilfordi* still persists compared to those where *M. martes* has replaced it as seed disperser. Our analysis in this study of the patterns of seed dispersal by *P. lilfordi* vs. *M. martes*, the density of seeds finally achieved in different sites and the suitability of these sites for seedling emergence and survival in early life stages sheds more light on the consequences of the extinction of *P. lilfordi* and their replacement by *M. martes* in some populations. It also allows us to discern the causes of the recruitment limitation observed, as by a deficit of seed dispersal or by a low suitability of sites. The extinction of *P. lilfordi* in Mallorca seems to result in recruitment limitation by seed dispersal at the coastal shrubland but not at the pine forest, where *M. martes* replaces *P. lilfordi* as seed disperser, favouring recruitment in this habitat. The absence of seed dispersal in the coastal shrubland in Mallorca restricts seed arrival to under conspecifics. This clearly limits seedling

recruitment, which was c. four times lower in the coastal shrubland in Mallorca than in the coastal shrubland in Dragonera. In Dragonera, dispersal by *P. lilfordi* in the coastal shrubland favoured seed arrival to a variety of microhabitats outside the canopy of mother plants, and especially to open ground, where seed density reached similar values to those under *C. tricocon*. In addition, the suitability of open ground for seedling recruitment and survival was high, similar to that under mother plants. In contrast, in Mallorca, there was no recruitment in open ground, which has to be attributed to dispersal limitation.

In pine forests, in contrast, no seed limitation for recruitment was detected. The role of the introduced *M. martes* as seed disperser, replacing the extinct *P. lilfordi* in this service to plants, allowed seed arrival and recruitment outside mother plants. The contrasting patterns of seed dispersal by *P. lilfordi* and *M. martes* resulted, however, in differences in seed distribution between islands, with less seeds reaching open areas outside the pine canopy and more arriving under pine canopy in Mallorca, where *M. martes* instead of *P. lilfordi* acted as seed dispersers. These differences however were very slight and resulted also in slight differences in seedling distribution, as microhabitat suitability was similar between islands, both for seedling emergence and survival.

In conclusion, the extinction of *P. lilfordi* in Mallorca seriously limits recruitment in the coastal shrubland, the typical habitat of *C. tricocon*. Paradoxically, one of the introduced lizard predators that have probably contributed to its extinction has become the main seed disperser of *C. tricocon* in Mallorca. However, *M. martes* differs from *P. lilfordi* in many aspects, which leads to important differences in the dispersal service they provide. *Martes martes* has different habitat preferences: it is

absent in the coast and is mostly restricted to pine forests in mountain areas, an unfavourable habitat for *P. lilfordi*. On the other hand, *M. martes* has larger home ranges than *P. lilfordi*, which may favour gene flow and the colonization of new areas (Zalewski et al. 2004), although always restricted to the habitats they use. In the coastal shrubland, the lack of animal dispersal limits recruitment to under conspecifics, which may have serious consequences in the long term (e.g. Calviño-Cancela et al. 2012). The new recruits can only replace their mothers in the same site, but, whenever plants die and the site becomes empty, no re-colonization occurs due to dispersal limitation. Since the colonization of new sites is also precluded due to dispersal limitation, this marks an inescapable trend towards population shrinkage in the long term, which has led to the decline of these species in most of its former distribution (Traveset et al. 2012).

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References

- 370 Alcover JA (2008) The first mallorcans: prehistoric colonization in the western
371 Mediterranean. *Journal of World Prehistory* 21: 19–84
- 372 Bascompte J, Jordano P (2007) The structure of plant-animal mutualistic networks: the
373 architecture of biodiversity. *Annual Review of Ecology Evolution and*
374 *Systematics* 38: 567-593
- 375 Bauwens D, Hertz PE, Castilla AM (1996) Thermoregulation in a Lacertid Lizard: The
376 Relative Contributions of Distinct Behavioral Mechanisms. *Ecology* 77: 1818-
377 1830
- 378 Calviño-Cancela M (2002) Spatial patterns of seed dispersal and seedling recruitment in
379 *Corema album* (Empetraceae): The importance of unspecialized dispersers for
380 regeneration. *Journal of Ecology* 90: 775-784
- 381 Calviño-Cancela M (2007) Seed and microsite limitations of recruitment and the
382 impacts of post-dispersal seed predation at the within population level. *Plant*
383 *Ecology* 192: 35–44
- 384 Calviño-Cancela M, Martin-Herrero J (2009) Effectiveness of a varied assemblage of
385 seed dispersers of a fleshy-fruited plant. *Ecology* 90: 3503–3515
- 386 Calviño-Cancela M (2011a) Simplifying methods to assess site suitability for plant
387 recruitment. *Plant Ecology* 212: 1375–1383
- 388 Calviño-Cancela M (2011b) Gulls (Laridae) as frugivores and seed dispersers. *Plant*
389 *Ecology* 212: 1149–1157
- 390 Calviño-Cancela M, Escudero M, Rodríguez-Pérez J, Cano E, Vargas P, Velo-Antón G,
391 Traveset A (2012) The role of seed dispersal pollination and historical effects on

392 genetic patterns of an insular plant that has lost its only seed disperser. Journal of
393 Biogeography 39: 1996–2006

394 González-Castro A, Traveset A, Nogales M (2012) Seed dispersal mutualistic
395 interactions in the Mediterranean Region: contrasting patterns between islands
396 and mainland. Journal of Biogeography 39: 1938–1947

397 Gunn B (2001) Australian tree seed centre operations manual. CSIRO Forestry and
398 Forest Products, Canberra.

399 Herrera CM (1989) Frugivory and seed dispersal by carnivorous mammals and
400 associated fruit characteristics in undisturbed Mediterranean habitats. Oikos: 55
401 250-262

402 Herrera CM, Jordano P, López-Soria L, Amat JA (1994) Recruitment of a mast-fruiting
403 bird-dispersed tree. Bridging frugivore activity and seedling establishment.
404 Ecological Monographs 64: 315-344

405 Harper JL (1977) Population biology of plants. Academic Press London.

406 Jobidon R (1993) Nitrate fertilization stimulates emergence of red raspberry (*Rubus*
407 *idaeus* L.) under forest canopy. Nutrient Cycling in Agroecosystems 36: 91-94

408 Kelly D, Ladley JJ, Robertson AW, Anderson SH, Wotton DM, Wiser SK (2010)
409 Mutualisms with the wreckage of an avifauna: the status of bird pollination and
410 fruit-dispersal in New Zealand. New Zealand Journal of Ecology 34: 66–85

411 McKinney ST, Fiedler CE, Tomback DF (2009) Invasive pathogen threatens bird-pine
412 mutualism: implications for sustaining a high-elevation ecosystem. Ecological
413 Applications 19:597-607

414 Martínez I, García D, Obeso JR (2008) Differential seed dispersal patterns generated by
 415 a common assemblage of vertebrate frugivores in three fleshy fruited trees.
 416 *Ecoscience* 15: 189-199

417 Mortensen HS, Dupont YL, Olesen JM (2008) A snake in paradise: Disturbance of plant
 418 reproduction following extirpation of bird flower-visitors on Guam. *Biological*
 419 *conservation* 141: 2146–2154

420 Olesen J, Jordano P (2002) Geographic patterns in plant-pollinator mutualistic
 421 networks. *Ecology* 83: 2416-2424

422 Pérez-Mellado, V (2002) *Podarcis lilfordi*. In: J.M. Pleguezuelos, R. Márquez and M.
 423 Lizana (ed) *Atlas y libro rojo de los anfibios y reptiles de España*. Dirección
 424 General de Conservación de la Naturaleza-Asociación Herpetológica Española,
 425 Madrid. pp. 248–250.

426 Pérez-Mellado V, Hernández-Estévez JA, García-Díez T, Terrassa B, Ramón MM,
 427 Castro J, Picornell A, Martín-Vallejo J, Brown R (2008) Population density in
 428 *Podarcis lilfordi* (Squamata Lacertidae) a lizard species endemic to small islets
 429 in the Balearic Islands (Spain). *Amphibia-Reptilia* 29: 49-60

430 R Development Core Team (2008) R: A language and environment for statistical
 431 computing. R Foundation for Statistical Computing, Vienna, Austria. URL
 432 <http://www.R-project.org>

433 Reumer JWF, Sanders EAC (1984) Changes in the vertebrate fauna of Menorca in
 434 prehistoric and classical times. *Z Säugetierkunde* 49: 321–325

- 435 Riera N, Traveset A, García O (2002) Breakage of mutualisms by exotic species: the
436 case of *C. tricocon* L. in the Balearic Islands (Western Mediterranean Sea).
437 *Journal of Biogeography* 29: 713–719
- 438 Rey PJ, Alcántara J (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea*
439 *europaea*): connecting patterns of seed dispersal to seedling establishment.
440 *Journal of Ecology* 88: 622–633
- 441 Rodríguez-Pérez J, Traveset A (2012) Demographic consequences for a threatened plant
442 after the loss of its only disperser. Habitat suitability buffers limited seed
443 dispersal. *Oikos* 121: 835–847.
- 444 Rosalino LM, Santos-Reis M (2009) Fruit consumption by carnivores in Mediterranean
445 Europe. *Mammal Review* 39: 67–78
- 446 Schupp EW (1993) Quantity quality and the effectiveness of seed dispersal by animals.
447 *Vegetatio* 107/108: 15–29
- 448 Schupp EW, Fuentes M (1995) Spatial patterns of seed dispersal and the unification of
449 plant population ecology. *Ecoscience* 2: 267–275
- 450 Schupp EW (2007) The suitability of a site for seed dispersal is contextdependent. *In*:
451 Dennis AJ, Schupp EW, Green RJ, Westcott DA, eds. *Seed dispersal: theory and*
452 *its application in a changing world*. CAB International, Wallingford, UK, pp 445–
453 462
- 454 Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a
455 conceptual review. *New Phytologist* 188: 333–353

456 StatSoft Inc. (2004) STATISTICA for Windows. Manual version 7.0. StatSoft Inc.,
 457 Tulsa, Oklahoma

458 Terrasa B, Pérez-Mellado V, Brown RP, Picornell A, Castro JA, Ramon MM (2009)
 459 Foundations for conservation of intraspecific genetic diversity revealed by
 460 analysis of phylogeographical structure in the endangered endemic lizard
 461 *Podarcis lilfordi*. Diversity and Distributions 15: 207–221

462 Traveset A, Quintana J, Alcover JA (2005) Fossil seeds from the Pliocene of Menorca
 463 and Eivissa (Balearic Islands, western Mediterranean). Endins 27: 205–209

464 Traveset A (1995a) Seed dispersal of *Cneorum tricoccon* by lizards and mammals in the
 465 Balearic Archipelago. Acta Oecologica 16: 171-178

466 Traveset A (1995b) Reproductive ecology of *Cneorum tricoccon* L. (Cneoraceae) in the
 467 Balearic Islands. Botanical Journal of the Linnean Society 17: 221-232

468 Traveset A, Sáez E (1997) Pollination of *Euphorbia dendroides* by lizards and insects:
 469 spatio-temporal variation in patterns of flower visitation. Oecologia 111: 241-
 470 248

471 Traveset A, Bermejo T, Willson M (2001) Effect of manure composition on seedling
 472 emergence and growth of two common shrub species of Southeast Alaska. Plant
 473 Ecology 155: 29-34

474 Traveset A, Gulias J, Riera N, Mus M (2003) Transition probabilities from pollination
 475 to establishment in a rare dioecious shrub species (*Rhamnus ludovici-salvatoris*)
 476 in two habitats. Journal of Ecology 91: 427–437

477 Traveset A, Riera N (2005) Disruption of a plant-lizard seed dispersal system and its
 478 ecological consequences for a threatened endemic plant in the Balearic Islands.
 479 Conservation Biology 19: 421-431

480 Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant-animal
 481 reproductive mutualisms. Trends in Ecology and Evolution 21: 208-216

482 Traveset A, Nogales M, Alcover JA, Delgado JD, López-Darias M, Godoy D, Igual JM,
 483 Bover P (2009) A review on the effects of alien rodents in the Balearic (Western
 484 Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). Biological
 485 Invasions 11: 1653–1670

486 Traveset A, González-Varo JP, Valido A (2012) Long-term demographic consequences
 487 of a seed dispersal disruption. Proceedings of the Royal Society B 279:3298-
 488 3303

489 Zalewski A, Jedrzejewski W, Jedrzejewska B (2004) Mobility and home range use by
 490 pine martens (*Martes martes*) in a Polish primeval forest. Ecoscience 11: 113-
 491 122

Table 1. Table of results of three independent nested GLM to analyse the effect of island, habitat and microhabitat (with microhabitat nested in habitat and both nested in island) on the density of total seeds, the proportion of predated seeds and the density of viable seeds.

	Total seeds			Predated seeds (%)		Viable seeds	
	df	Deviance	P	Deviance	P	Deviance	P
Island	1	511.41	0.029	47.814	<0.001	6.6	0.7
Habitat	2	1310	0.002	47.343	0.626	369.4	0.017
Microhabitat	8	934.09	0.372	40.271	0.080	583.1	0.1

Table 2. Table of results of three independent nested GLM to analyze the effect of island, habitat and microhabitat (with microhabitat nested in habitat and both nested in island) on seedling density, seedling/seed ratio and seedling transition probability.

	Total seedlings			Seedling/seed ratio			Seedling transition		
	df	Deviance	P	df	Deviance	P	df	Deviance	P
Island	1	9.27	0.39	1	1.00	0.13	1	3663.6	0.088
Habitat	2	359.94	<0.001	2	53.07	<0.001	2	3640.1	0.094
Microhabitat	8	716.56	<0.001	7	779.82	<0.001	5	3600.1	0.007

Fig. 1. Mean density of faeces (white bars left axis) and seedlings (black bars right axis) on different microhabitats in the coastal shrubland (A and C) and in the pine forest (B and D) in Dragonera and Mallorca respectively. Solid and dashed lines represent the expected density of faeces and seedlings, respectively, according to a random distribution among microhabitats.

Fig. 2. Density (mean \pm SE) of seeds (left axis) with total (white bars), viable (diagonal lines bars) and predated (crossed lines) seeds, and seedlings (black bars right axis) at each microhabitat in the coastal shrubland (A and C) and in the pine forest (B and D) in Mallorca and Dragonera, respectively. Different letters on top of bars indicate statistically different values among microhabitats for each variable.

Fig. 3. Seedling/seed ratio (white bars) and the ratio between seedling stages (black bars) (mean \pm SE) at each microhabitat in the coastal shrubland (A and C) and in the pine forest (B and D) in Mallorca and Dragonera, respectively. Different letters on top of bars indicate statistically different values among microhabitats for each variable. Notice the absence of data for open ground in Mallorca due to the lack of seeds and seedlings in this microhabitat.





